



Richness and composition of macrophyte assemblages in four Amazonian lakes

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ABSTRACT. Aquatic macrophytes are an important component in the structure of lakes in Neotropical floodplains, for example, because they support a high diversity of invertebrates and vertebrates. In this paper, we tested whether or not the variability of macrophyte assemblages is lower in spatially close quadrats than among quadrats of different lakes. The study was carried in four lakes in a large Amazonian floodplain (Purus river), where floating meadows were investigated. A total of 49 taxa of macrophytes were found. Five species dominated and three species were rare. Taxa richness, composition and beta diversity differed more between than within lakes. Because high beta diversity was found among the lakes, they should be considered individually important for maintaining the gamma diversity of macrophytes within the Purus River floodplain, and this should be considered in plans of lake management.

Keywords: Purus river, oxbow lake, dry season, Amazon, floating meadows, diversity.

Riqueza e composição da assembleia de macrófitas em quatro lagos amazônicos

RESUMO. As macrófitas aquáticas são um importante componente para a estrutura de lagos neotropicais em planícies de inundação, porque suportam alta diversidade de invertebrados e vertebrados. Neste trabalho, nós testamos se a variabilidade da assembleia de macrófitas aquáticas é menor entre “quadrats” espacialmente próximos do que “quadrats” em lagos diferentes. O estudo foi desenvolvido em quatro lagos da planície amazônica (rio Purus), onde bancos flutuantes de macrófitas foram amostrados. Um total de 49 taxa de macrófitas foi encontrado. Cinco espécies dominaram e três espécies foram raras. A riqueza de taxa, composição e diversidade de espécies diferiram mais entre os lagos do que dentro dos lagos. Pela alta diversidade beta encontrada nos lagos, esses lagos devem ser considerados importantes individualmente para manter a diversidade gamma de macrófitas dentro da planície de inundação do rio Purus. Esse fato deve ser considerado em planos de manejo desses lagos de planície.

Palavras-chave: rio Purus, lagos em ferradura, estação seca, Amazônia, baceiros, diversidade.

Introduction

Aquatic and semi-aquatic herbaceous plants colonize a variety of aquatic and transitional habitats in Neotropical floodplains (MALTCHIK et al., 2007; JUNK; PIEDADE, 1993; PIEDADE; JUNK, 2000). These plants are highly productive and diverse, and they are key to maintaining the diversity of invertebrates (e.g., PEIRÓ; ALVES, 2006; HIGUTI et al., 2009; LANSAC-TÔHA et al., 2009) and vertebrates (e.g., PELICICE; AGOSTINHO, 2006; PETRY et al., 2003; CANTO-MAZA; VEGACENDEJAS, 2008) in several freshwater ecosystems, including the Amazonian lakes, canals and main river channels (JUNK, 1986; JUNK; PIEDADE, 1993; PIEDADE; JUNK, 2000).

In the Amazonian floodplains, floating meadows are a very common formation. These islands are

mainly composed of grasses; they are found in several different types of habitats and are commonly seen drifting down the rivers (JUNK, 1970). Like macrophytes in general, the importance of floating meadows to aquatic fauna is also well recognized in the Amazon region (e.g., PIEDADE; JUNK, 2000; PETRY et al., 2003).

The patterns of diversity at different spatial scales are among the main issues investigated by ecologists in recent decades. For macrophytes, for example, it has been shown that richness, diversity (both alpha and beta) and composition usually vary within a single lake, between lakes in the same region and among lakes in different regions of a floodplain (e.g., BINI et al., 2001). Over different scales, this variation contributes to the gamma diversity (i.e., the diversity of an entire ecosystem or regional diversity).

Lakes are important habitats in floodplains because they maintain permanent water tables and thus constitute appropriate habitats for aquatic flora and fauna, even during low water periods (FERNANDES et al., 2009). Due to low flow, these lakes are propitious for macrophyte colonization. Despite the existence of thousands of lakes in river floodplains in the Amazon region, investigations on macrophytes are relatively rare. The few existing studies were carried out in the Solimões and Negro rivers habitats and in the central Amazon, in the Manaus region (e.g., JUNK, 1986; JUNK; PIEDADE, 1993; PIEDADE; JUNK, 2000).

In this investigation, we assessed the richness and composition of macrophyte assemblages in four lakes associated with the Purus River (State of Amazonas, Brazil). We tested the hypothesis that, despite being spatially close (maximum of ca. 15 km apart) and associated with the same river (Purus river), the variability in macrophyte assemblages among lakes is higher than among quadrats in the same lake. If true, this pattern has implications for beta and gamma diversity of macrophytes in the Purus floodplain, and, consequently, for their management plans.

Material and methods

Study area

The study was carried out in four lakes (Bom Lugar, Verde, Samauminha and Timba) located in the floodplain of the upper Purus river (Figure 1). These lakes are positioned from 0.7 km (Lake Timba) to 1.7 km (Bom Lugar) from the river channel during the low water phase. During this phase, the approximate lengths and depths are 6.0×0.24 km (Lake Bom Lugar), 6.3×0.2 km (Lake Verde), 0.5×0.3 km (Lake Samauminha) and 0.7×0.2 km (Lake Timba).

During the sampling period, the water of River Purus was close to its lowest level; the decline started approximately three months earlier (i.e., in March). Due to their location close to the river and a direct connection through both channels and/or overbank flow during high water periods, these lakes are supposedly fertilized by the River Purus, which exhibits high concentrations of solids, nitrogen and phosphorus (ARAUJO-LIMA; RUFFINO, 2003). However, unlike the river main channel, all lakes had yellowish-black waters, characteristic of a high humic content.

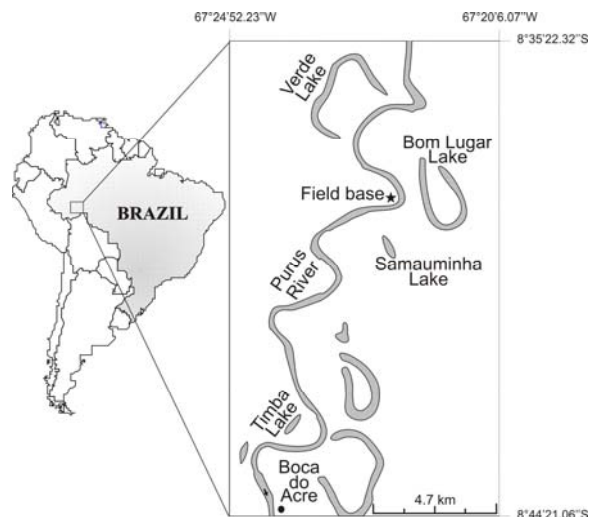


Figure 1. Map of the studied area showing the four lakes investigated.

Sampling

Sampling was carried out from 1st to 3rd July 2009. Macrophyte abundances were assessed by visual estimates of the percentage cover of each species inside a 0.5×0.5 m quadrat, which was transformed into a scale based on Braun-Blanquet (1: < 5%; 2: 6-25%; 3: 26-50%; 4: 51-75; 5: 76-100%). We analyzed a total of 60 quadrats (15 per lake). In addition to the quadrats, macrophytes in the littoral region were also visually inspected from a boat. Macrophytes that could not be identified in the field were collected and preserved as herbarium samples for subsequent identification (POTT; POTT, 2000; LORENZI, 2000; KISSMAN, 1997) at the Plant Ecology Laboratory of the Federal University of Acre. Approximately 35% of the taxa could not be identified to species level due to the lack of reproductive structures. Due to the predominance of floating meadows, it was difficult to collect plants along the shores; therefore, our survey mainly refers to the species of macrophytes that were growing on or close to these meadows.

The relative importance of each family and life form was estimated as frequency of occurrences, calculated as the number of quadrats in which they were found divided by the total number of quadrats (60). Life forms were based on Pedralli (2003): emergents (macrophytes that grow in water but support slightly wet soils too; herein referred to as "emergents"), free floating (macrophytes not rooted in the sediment), epiphytes (plants growing attached to other macrophytes), rooted submersed (totally submersed but rooted in the sediment) and free submersed (macrophytes anchored onto other macrophytes or onto submersed structures).

Data analysis

Because sampling may hide true differences between species richness among ecosystems or sampling stations (GOTELLI; COLWELL, 2001), we used accumulation curves to compare taxa richness (S) among the four lakes. The curves were also indicative of whether or not our sampling was effective. Accumulation curves were drawn using the quadrats as units in the program EstimateS (COLWELL, 2006).

To estimate the richness of macrophytes found in the quadrats, we applied three non-parametric extrapolating indices: S_{jack1} , S_{ice} , and S_{Cao2} . These indices are based on incidence (presence/absence) data (CHAZDON et al., 1998) and we used quadrats as our sampling units. Previous investigations with macrophytes showed that they approach the real number of species found in intensive investigations and they are thus adequate for estimating diversity when incidence data are used (BINI et al., 2001).

We summarized the data set with a detrended correspondence analysis (DCA). Quadrats were used as sampling units and the Braun-Blanquet scale as a surrogate of the abundance values of

each taxon. The inspection of a figure constructed with the first two DCA axes helped identify spatial patterns of macrophyte assemblages and the dispersion of points (an indication of beta diversity) in each lake and between lakes. The most important species to the ordination axes were identified using the correlation with the main matrix available in PC-ORD (MCCUNE; MEFFORD, 1999). This analysis correlates species scores with their abundances in the original data matrix. In addition, scores of the first two axes were generated and tested for differences among lakes (factor in ANOVA terminology) using one-way ANOVA.

Results

We recorded a total of 49 taxa of macrophytes belonging to 29 families when sampling inside quadrats and in the lake surveys (Table 1). The number of taxa per lake ranged from 21 (Samauminha Lake) to 29 (Verde Lake). Cyperaceae was the most important family, both in the number of taxa (eight; Table 1) and the frequency of occurrence (Figure 2a)..

Table 1. Macrophyte taxa. LF = life forms, Em = emergent, Am = amphibious, FF = free floating, Ep = epiphyte, RS = rooted submersed, FS = free submersed.

Taxa	Bom Lugar	Verde	Samauminha	Timba	LF
Ricciaceae					
<i>Ricciocarpus natans</i> (L.) Corda	x				FF
Aspleniaceae					
<i>Asplenium</i> sp.				x	Am
Azollaceae					
<i>Azolla</i> sp.	x			x	FF
Polypodiaceae					
<i>Polypodium</i> sp.		x	x		Am
Pteridaceae					
<i>Adiantum</i> sp.				x	Am
<i>Ceratopteris pteridoides</i> (Hook.) Hieron.	x				FF
Pteridaceae					
<i>Pityrogramma calomelanos</i> (L.) Link		x		x	Am
Pteridaceae					
<i>Pteris</i> sp.				x	Am
Salviniaceae					
<i>Salvinia auriculata</i> Aublet	x	x	x	x	FF
<i>Salvinia minima</i> Bak.	x	x	x	x	FF
Thelypteridaceae					
<i>Thelypteris</i> sp.			x		Am
Amaranthaceae					
<i>Alternanthera philoxeroides</i> (Mart.) Griseb.	x	x	x	x	Am
Apiaceae					
<i>Hydrocotyle ranunculoides</i> L. f.		x			Em
Araceae					
<i>Pistia stratiotes</i> L.	x	x	x	x	FF
Asteraceae					
<i>Eclipta alba</i> (L.) Hassk.	x				Am
<i>Enydra anagallis</i> Gardner	x		x	x	Am
Begoniaceae					
<i>Begonia</i> sp.			x	x	Am
Ceratophyllaceae					
<i>Ceratophyllum</i> sp.		x			RS
Convolvulaceae					
<i>Ipomoea</i> sp.	x				Am
Cyperaceae					
<i>Cyperus ferax</i> Rich.		x			Am
<i>Cyperus haspan</i> L.		x			Am

Continue...

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Taxa	Bom Lugar	Verde	Samauminha	Timba	LF
<i>Cyperus luzulae</i> (L.) Rottb. ex Retz.		x			Am
<i>Cyperus</i> sp.	x				Am
<i>Eleocharis</i> sp.		x	x		Em
<i>Fuirena</i> cf. <i>umbellata</i> Rottb.			x		Em
<i>Oxycaryum cubensis</i> (Poepp and Kunth.) Lye	x	x	x	x	Ep
<i>Pycnus</i> sp.		x			Am
Euphorbiaceae					
<i>Phyllanthus fluitans</i> Benth. ex Müll. Arg.		x	x	x	FF
Fabaceae					
<i>Aeschynomene</i> sp.	x				Am
Fabaceae					
<i>Vigna</i> sp.	x	x		x	Ep
Hydrocharitaceae					
<i>Limnobiium laevigatum</i> (Humb. and Bonpl. ex Willd.) Heine	x	x	x		FF
Lemnaceae					
<i>Lemna</i> sp.	x	x	x	x	FF
<i>Wolffella lingulata</i> Hegelm.	x	x		x	FF
Lentibulariaceae					
<i>Utricularia</i> cf. <i>gibba</i> L.	x	x			FS
Malvaceae					
<i>Hibiscus sororius</i> L.		x			Am
Onagraceae					
<i>Ludwigia helminthorrhiza</i> (Mart.) H. Hara	x	x	x	x	FF
<i>Ludwigia leptocarpa</i> (Nutt.) H. Hara	x			x	Am
<i>Ludwigia nervosa</i> (Poir.) H. Hara	x				Am
<i>Ludwigia</i> sp.		x		x	Am
Orchidaceae					
<i>Habenaria</i> cf. <i>repens</i> Nutt.				x	Am
Poaceae					
<i>Andropogon bicornis</i> L.		x	x		Am
<i>Echinochloa</i> sp.			x		Em
<i>Paspalum repens</i> Berg.	x	x	x		Em
Polygonaceae					
<i>Polygonum acuminatum</i> Kunth		x	x		Em
<i>Polygonum ferrugineum</i> Wedd.				x	Em
Pontederiaceae					
<i>Eichhornia crassipes</i> (Mart.) Solms.	x	x	x	x	FF
Rubiaceae					
<i>Psychotria</i> sp.		x			Am
Urticaceae					
<i>Boehmeria</i> sp.		x			Am
Verbenaceae					
<i>Lippia alba</i> (Mill.) N.E. Br.	x		x		Am

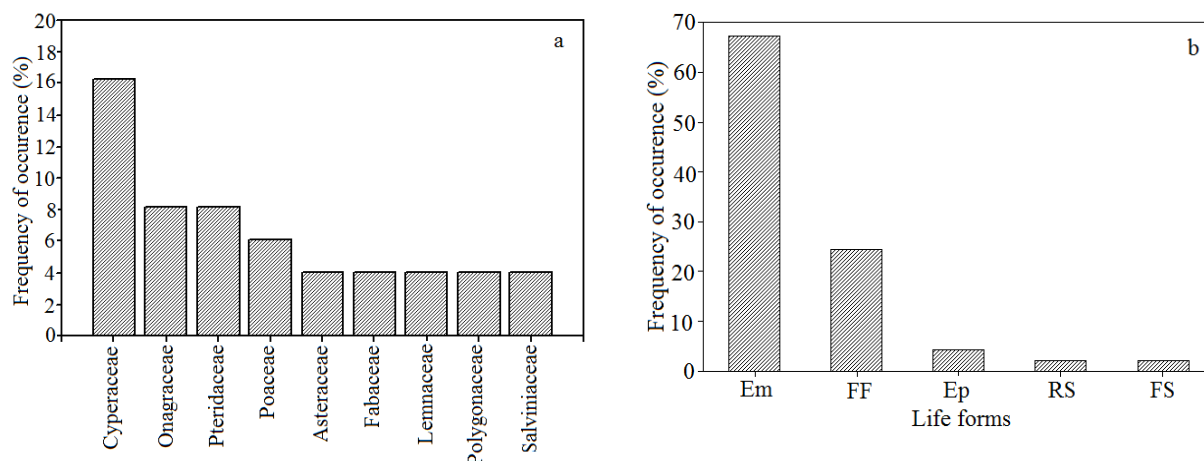


Figure 2. Frequency of occurrence of the different families (a) and macrophyte life forms (b) in the four lakes sampled. Em = emergent, FF = free floating, Ep = epiphyte, RS = rooted submersed, FS = free submersed.

We recorded 29 species inside the 60 quadrats sampled in the floating meadows, which were dominated by five species, with the following frequency of occurrences: *Salvinia minima* Aubl. (78%), *Eichhornia crassipes* (Mart.) Solms, *Ludwigia*

helminthorrhiza (Mart.) H. Hara and *Pistia stratiotes* L. (52%), and *Oxycaryum cubense* (Poepp. and Kunth) Palla (49%). Three species were rare, occurring in only 1 out of 60 quadrats (*Habenaria* cf. *repens* Nutt., *Lippia alba* (Mill.) N.E. Br. and *Ricciocarpos natans* (L.) Corda).

The use of extrapolating indices showed that the richness found in the quadrats was underestimated in less than 10% ($S_{jack1} = 31.9$ species; $S_{ice} = 30$ species; $S_{Cao2} = 31.9$ species). Considering the frequency of occurrence of the different life forms, emergents were the most important, and free-floating species the second most important group (Figure 2b). Rooted-submersed and free-submersed species were unimportant in terms of occurrence (Figure 2b).

Cumulative curves with quadrats as units showed that an asymptote was reached in all lakes (Figure 3). Similar to what we found for the total number of species, the lowest richness appeared in Lake Samauminha while the highest richness was found in Lake Bom Lugar (Figure 3).

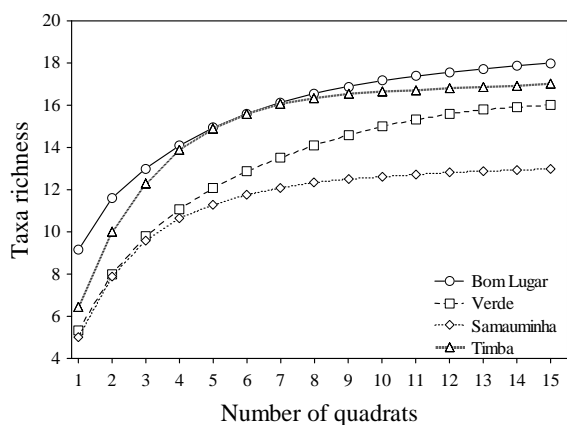


Figure 3. Cumulative curves of macrophytes found in four Amazonian lakes.

In fact, significant differences among lakes were found when testing the scores of both axes (Figure 4b and c). In addition to separate lakes, the score dispersion (seen through standard errors in Figure 4b and c) also indicated great differences in beta diversity among the lakes. Bom Lugar, with the lowest dispersion of quadrats, was the lake where quadrats were less dissimilar, whereas Timba Lake, with the highest dispersion, had the most dissimilar quadrats.

The macrophyte assemblage structure (summarized by a DCA) mainly showed a distinction between Samauminha and Timba (along axis 1) and Bom Lugar and Verde lakes (along axis 2) (Figure 4a).

In general, the taxa that contributed most to axis 1 were *Echinochloa* sp. ($r = -0.44$), *Phyllanthus fluitans* Benth. ex Müll. Arg. ($r = -0.41$), *Vigna* sp. ($r = 0.64$), *O. cubense* ($r = 0.58$) and *Ludwigia* sp. ($r = 0.53$). To discriminate between quadrats along axis 2, the most important taxa were *L. helminthorrhiza* ($r = 0.54$), *Lemna* sp. ($r = -0.67$), *Azolla* sp. ($r = -0.63$), and *Wolffia lingulata* Hegelm. ($r = -0.63$) (Figure 4a).

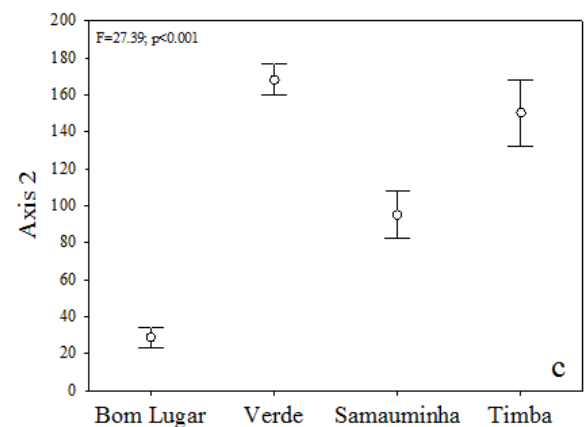
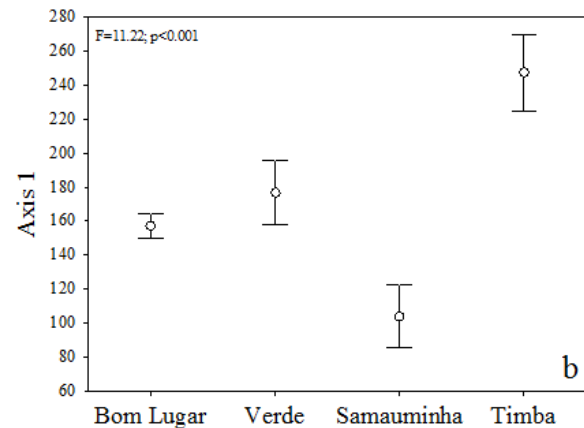
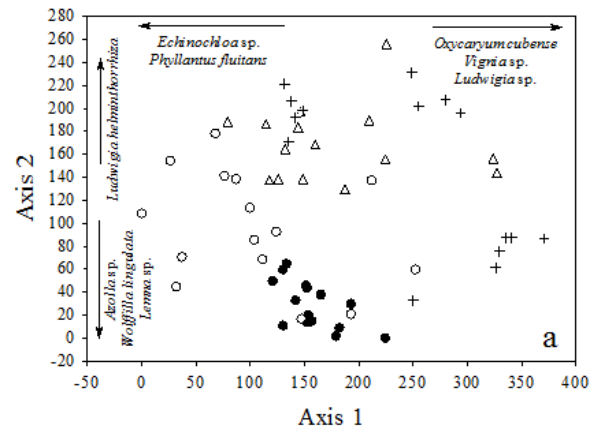


Figure 4. Ordination of the macrophyte assemblages in four Amazonian lakes, using the first two DCA axes. Each symbol represents a quadrat. Black circle: Lake Bom Lugar; empty circle: Lake Samauminha; triangle: Lake Verde; cross: Lake Timba (a). Means and standard errors of the DCA axis 1 (b) e axis 2 (c) are also shown.

Discussion

The floating meadows contained a mixture of macrophyte life forms, with a dominance of emergent and free-floating species. The most frequently found macrophyte species in the Purus lakes (*E. crassipes*, *S. minima* and *P. stratiotes*) are also important in other freshwater ecosystems of the Amazon region (JUNK; PIEDADE, 1993; PIEDADE; JUNK, 2000; PETRY

et al., 2003), but they differ from other floodplains located in South Brazil or even in the Pantanal (one of the biggest wetlands in the world), where the floating-stem macrophytes *Eichhornia azurea* (Sw.) Kunth are usually the principal species (e.g., SILVA; PINTO-SILVA, 1989; MALTCHIK et al., 2007; THOMAZ et al., 2009).

The taxa richness per lake (21-29 taxa) is within the values found in several other Neotropical floodplain lakes (e.g., MALTCHIK et al., 2007; THOMAZ et al., 2009). The total richness (49 taxa) recorded in the four lakes is also similar to that found in floating meadows in other Amazonian white water rivers, such as the ones near Manaus (45 species; JUNK; PIEDEDE, 1993).

According to our extrapolating indices, the richness found in the floating meadows approached the real richness. However, considering that our survey was the result of a single sampling event and that it was basically restricted to floating meadows, it is certain that the total taxa richness of macrophytes for the entire lakes was underestimated. Additional sampling encompassing other habitats in littoral zones, and on coarser spatial and longer temporal scales, would certainly add other species to these lakes. For example, by also sampling the *várzea* of the Amazon River, a total of 388 species of herbaceous vegetation was found, most of them occurring in semi-aquatic habitats (JUNK; PIEDEDE, 1993). On the other hand, compared to black and clear water systems in the Amazon basin, the species richness of assemblages found in white water rivers (like the ones we found in the River Purus lakes) is higher, as black waters have a lower nutrient status and pH values (JUNK, 1986; PIEDEDE; JUNK, 2000).

The predominance of emergent/amphibian macrophytes is an expected finding in Neotropical floodplains. In general, these life forms predominate in several types of aquatic ecosystems all over the Neotropics (e.g., POTT; POTT, 2000; THOMAZ et al., 2009), including Amazonian floodplain lakes (JUNK; PIEDEDE, 1993). However, it is worth noting that free-floating species were the second most important group in terms of frequency of occurrence, and they were also important in terms of the number of species (12 species). The elevated frequency and richness of this group may be directly associated with the high nutrient status of the lakes investigated, because the River Purus exhibits high solid and nutrient contents (ARAUJO-LIMA; RUFFINO, 2003). On the other hand, the high solid contents during high waters, together with high humic contents during low waters (as observed in all four lakes), indicate that under-water radiation

can be limiting in these lakes. As a consequence, rooted-submersed species were very rare in our samples (only one species).

The structure of macrophyte assemblages is highly affected by water level fluctuations in floodplains, like in the one we investigated (e.g., PIEDEDE; JUNK, 2000; MALTCHIK et al., 2007; NEIFF et al., 2008). Despite only undertaking one sampling, during the low water phase, we may speculate about some outcomes of our investigation. For example, in general, assemblages occurring in floodplain lakes (including macrophytes) tend to show different successional pathways in distinct lakes during low water phases, when they become isolated from the main river and are largely affected by local driving forces (THOMAZ et al., 2007). This particularly holds true for the Amazonian lakes, because short-living organisms (like macrophytes) grow very fast under elevated temperatures (JUNK; PIEDEDE, 1993) and high nutrient contents, as typically found in the River Purus (ARAUJO-LIMA; RUFFINO, 2003). Lake isolation followed by different successions during low waters probably explain the quite distinct assemblages we found in the four lakes, both in terms of taxa richness (see Figure 3 and Table 1) and structure (see Figure 4). It is worth noting that significant differences in richness and structure (as demonstrated by DCA scores) were found even though the lakes are located within a short distance of each other (maximum 15 km).

In addition to clear differences in macrophyte diversity and composition, the lakes also differed in relation to beta diversity. This attribute can be defined as the 'turnover in species identity among localities within regions' (HARRISON et al., 1992) and it is usually positively affected by habitat heterogeneity (BINI et al., 2001). Thus, we may suppose that environmental gradients important for the determination of macrophyte assemblage structures vary from lake to lake. This characteristic enhances the habitat diversity at coarser spatial scales.

Conclusion

In conclusion, despite close proximity and nearness to the same river, the assemblages of each lake differed in taxa richness, structure and beta diversity. As a consequence of the high beta diversity among the lakes, their individual contribution is important for maintaining the gamma diversity of macrophytes within the Purus river floodplain. Local residents, who depend on fisheries, complain about excessive macrophyte cover and plant management is not discarded by environmental authorities. However, our conclusion about the importance of individual lakes for

maintaining gamma diversity should be taken into consideration by potential lake managers.

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